SHORTER ARTICLES AND DISCUSSION

FORMULÆ FOR THE RESULTS OF INBREEDING

In connection with Pearl's recent valuable analyses of the results of inbreeding (1, 2, 3), a comparison of these results with those from self-fertilization is of interest. In my note on the latter (4), I gave a formula for the rate at which organisms become homozygotic through continued self-fertilization. This occurs more slowly in the various types of inbreeding, but Pearl gives no general formula for it. For purposes of comparison I have worked out from Pearl's data the general formula for the rate at which organisms become homozygotic through continued brother by sister mating; as such formulæ appear to be of permanent value, it is here given.[1] What the formula gives is, precisely, (1) the proportion of individuals that will be homozygotic for any given character after any number of unbroken generations of such inbreeding, (2) the average proportion of the characters of a given individual that will be homozygotic after any number of unbroken generations of such inbreeding. The numerical value so obtained may conveniently be called the coefficient of homozygosis.

The formula turns out to be a combination of the successive powers of 2, with the successive terms of the Fibonacci series, which appears in so curious a way in various natural phenomena. In this series every term is the sum of the two preceding terms, the series beginning: 0, 1, 1, 2, 3, 5, 8, 13, etc.

Let $x =$ the coefficient of homozygosis.

$n =$ the number of inbred generations (the number of times successive brother by sister mating has occurred).

f_1, f_2, f_3, etc., $=$ the successive terms of the Fibonacci series (thus $f_1 = 0$, $f_2 = 1$, etc.).

Then the formula for the coefficient of homozygosis is:

$$x = \frac{2^{n-1} + f_1 \cdot 2^{n-2} + f_2 \cdot 2^{n-3} \ldots \text{etc.}}{2^n}$$

(The terms in the numerator are continued until the exponent of 2 becomes 0.)

[1] In conversation, Dr. Pearl urged the publication of the present note, otherwise I should not at this time have dealt with a matter which he has under analysis.

Thus, if the number of inbreedings (n) is 1.

$$x = \frac{2^0}{2^1} = 1/2, \text{ or } 50 \text{ per cent.}$$

If $n = 4$

$$x = \frac{2^3 + 0.2^2 + 1.2^1 + 1.2^0}{2^4} = 11/16, \text{ or } 68.75 \text{ per cent.}$$

If $n = 9$

$$x = \frac{2^8 + 0.2^7 + 1.2^6 + 1.2^5 + 2.2^4 + 3.2^3 + 5.2^2 + 8.2^1 + 13.2^0}{2^9}$$

$$= 457/512, \text{ or } 89.26 \text{ per cent.}$$

If $n = 16$

$$x = \frac{63819}{65536} \text{ or } 97.38 \text{ per cent.}$$

As these examples show, the formula gives the results that were obtained by Pearl in the detailed working out (so far as this was carried), as given in Pearl's table I (2, p. 62). (It will be noted that Pearl counts as generation *1* the one *before* inbreeding has occurred, so that his generation 10, for example, is that in which there have been 9 inbreedings $(n = 9)$.)

If one is working out the values of the coefficient x for a series of generations, the above formula may be expressed as a simple rule, applicable after the value for $n = 1$ is obtained. This rule is:

The value of the coefficient of homozygosis x for any term (as the nth) is obtained by doubling the numerator and denominator of the fraction expressing the value for the previous term, and adding to the numerator the corresponding $(n — 1th)$ term of the Fibonacci series.

Or, in view of the peculiar nature of the Fibonacci series, the rule may be expressed as follows:

Double the numerator and denominator, and add to the numerator the sum of the last two numbers so added.

Thus, since

$$x \text{ for 1 inbreeding} = 1/2$$

$$x \text{ '' } 2 \text{ '' } = \frac{2 \times 1 + 0}{2 \times 2} = 2/4$$

$$x \text{ '' } 3 \text{ '' } = \frac{2 \times 2 + 1}{2 \times 4} = 5/8$$

$$x \text{ '' } 4 \text{ '' } = \frac{2 \times 5 + 1}{2 \times 8} = 11/16, \text{ etc.}$$

After obtaining x, or the proportion of homozygotes for any one pair of characters, the proportion y for any number m of pairs is obtained simply by raising x to the mth power, that is:

$$y = x^m.$$

Thus, after two generations of brother $\times$ sister mating, the proportion of homozygotes for three pairs of characters is $(1/2)^3 = 1/8$, or 12.5 per cent. After 8 generations of such inbreeding the proportion homozygotic for 10 pairs of characters is:

$$\left(\frac{222}{256}\right)^{10} = 24.05 \text{ per cent.}$$

The corresponding value in the case of continued self-fertilization is 99.61 per cent. (4, p. 491).

Whether it may be possible to obtain a similar formula for the coefficient of homozygosis in the cases of mating of cousin $\times$ cousin or of parent $\times$ offspring, remains to be discovered.

Pearl's ''coefficient of inbreeding'' gives the percentage of *lacking* ancestors in a given pedigree, as compared with the number that would be present if all the parents were unrelated. In order to compare self-fertilization with inbreeding in this respect, Pearl's formulæ for the coefficient of inbreeding may be expressed in terms of the number of successive inbreedings (n) for many purposes the formulæ appear more convenient so ex· pressed. The following gives these formulæ for self-fertilization and the three types of inbreeding, together with those, so far as worked out, for the proportion of individuals homozygotic with respect to a given character. In all these, n is the number of successive self-fertilizations or inbreedings.

Coefficient of Inbreeding.	Coefficient of Homozygosis.
Self-fertilization $\dfrac{2^n - 1}{2^n}$	$\dfrac{2^n - 1}{2^n}$
Brother $\times$ Sister $\dfrac{2^n - 2}{2^n}$	$\dfrac{2^{n-1} + f_1 \cdot 2^{n-2} + f_2 \cdot 2^{n-3} \cdots \text{etc.}}{2^n}$
Cousin $\times$ Cousin $\dfrac{2^{n-1} - 2}{2^n}$	?
Parent $\times$ Offspring $\dfrac{2^n - n - 1}{2^n}$	?

It will be observed that in self-fertilization the value of the coefficient of inbreeding is, curiously, the same as that of the coefficient of homozygosis, while in the other cases there is no evident simple relation between the two. Further, the coefficient

of inbreeding in brother $\times$ sister mating is the same as for self-fertilization, save that it lags one generation behind the latter; thus the coefficient for the fourth generation of self-fertilization is the same as that for the fifth of brother $\times$ sister mating. Pearl (1, p. 592) has already pointed out that in cousin mating the coefficient is one-half that for brother $\times$ sister, with a lag of one generation; as compared with self-fertilization the lag is two generations. No such simple relation is apparent between the proportions of homozygotes resulting from the diverse methods of breeding, though possibly such may yet be discovered.

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<div align="center">PAPERS CITED</div>

1. Pearl, R.   A contribution toward an analysis of the problem of inbreeding.   This Journal, XLVII, October, 1913, pp. 577–614.
2. ———.   On the results of inbreeding a Mendelian population; a correction and extension of previous conclusions.   This Journal, XLVIII, January, 1914, pp. 57–62.
3. ———.   On a general formula for the constitution of the nth generation of a Mendelian population in which all matings are of brother $\times$ sister.   This Journal, XLVIII, August, 1914, pp. 491–494.
4 Jennings, H. S.   Production of pure homozygotic organisms from heterozygotes by self-fertilization.   This Journal, XLVI, August, 1912, pp. 487–491.

A SHORT–CUT IN THE COMPUTATION OF CERTAIN PROBABLE ERRORS

In his handbook of statistical methods, on p. 38, Dr. C. B. Davenport[1] gives a short method for the calculation of the probable errors of some of the commonest statistical constants, in a table of logarithmic formulæ. It would seem that the simple and obvious short-cut involved has not been given the attention it deserves in connection with non-logarithmic calculation. The logarithmic formulæ are as follows:[2]

$$(1) \quad \log E_A = \log .6745 + \log \sigma - \tfrac{1}{2} \log n \left[\text{since } E_A = .6745 \frac{\sigma}{\sqrt{n}} \right],$$

$$(2) \quad \log E_\sigma = \log E_A - \tfrac{1}{2} \log 2 \left[\text{since } E_\sigma = .6745 \frac{\sigma}{\sqrt{2n}}, \text{ or, } E_\sigma = E_A \div \sqrt{2} \right],$$

[2] A indicates the weighted arithmetic mean, σ the standard deviation, and C the coefficient of variability.